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Effect of selection on shoot elongation rhythm of eastern white pine (*Pinus strobus* L.) and its implications to seed transfer in Ontario

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Abstract

Shoot elongation patterns of eastern white pine (*Pinus strobus* L.) from 112 natural populations in Ontario were studied for 2-year-old seedlings in a greenhouse and 7-year-old trees in a field provenance test. Shoot elongation curves were fitted with a logistic function for individual seedlings and trees, from which several shoot elongation rhythm variables were predicted. The effects of within population selection for increased growth on the shoot elongation rhythm variables were investigated at different selection intensities. Results indicate that faster growth in eastern white pine is associated with both an earlier start and later cessation of shoot elongation for individuals and populations. While among population variation is significant, from 83 to 92% of phenotypic variation in estimates of shoot elongation curve parameters and growth rhythm variables resides within populations, which tends to minimize the effects of geographic seed transfer on the synchronization between shoot growth rhythm and local climate. Within population, selections for increased growth can result in substantial change in population statistics of shoot growth rhythm variables. A selection intensity as low as 50% in height growth can delay shoot elongation cessation by nearly 6 days and expand the shoot elongation period by 8 days. The implications of changes in shoot elongation rhythms to seed transfer in Ontario are discussed.
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Keywords: *Pinus strobus*; Shoot elongation curve; Growth rhythm; Seed transfer

1. Introduction

Fast growth is usually considered a desirable characteristic to increase forest productivity. For tree species with large natural distribution, such as spruce and pine, populations of different geographic origins often grow at different rates when they are planted together (Fowler and Heimburger, 1969; Morgenstern and Mullin, 1990; Matyas and Yeatman, 1992; Morgenstern and Copis, 1998). Population differences in growth are, however, often accompanied with different patterns of growth rhythm (Li et al., 1993; Parker and Van-Niejenhuis, 1994; Johnsen et al., 1996). In several conifer species, southern populations were found to stop shoot elongation later than the local ones when planted at a northern site, while the northern populations tended to flush bud early when planted

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at a more southerly location (Ekberg et al., 1994; Westin, 1999; Partanen and Beuker, 1999). Population differentiation in growth rhythm is commonly attributed to the evolutionary adaptation of trees to, for example, thermal conditions and photoperiod, their local environments (Partanen and Beuker, 1999). Moving seeds too far from their natural origins in the temperate and boreal forests may cause undesirable consequences, such as growth rhythm not in pace with climate of the planting site, resulting in increased vulnerability to frost damage and potential loss of growth (Rehfeldt, 1979, 1992a; Matyas and Yeatman, 1992).

Individual trees within a natural population can differ in growth rhythm as well as growth rate. Selecting trees for faster growth within a local population can change growth rhythm of the population. For instance, Rehfeldt (1992a) found that strong selection for increased growth in *Pinus ponderosa* changed the growth rhythm to that typical of unselected populations from much milder environments. Extended growth periods resulting from selection for growth rate were also expected in other species, such as *Pinus banksiana* (Magnussen and Yeatman, 1989), *Pseudostuga menziesii* (Rehfeldt, 1983) and *Larix occidentalis* (Rehfeldt, 1992b), due to genetic correlation between growth rate and growth rhythm traits.

A question of practical importance in seed source planning for reforestation programs is how much of a change in growth rhythm is acceptable to maintain population adaptation while simultaneously maximizing growth. The answer may vary depending on species and regional climate. However, if the adaptation of a natural population approaches near optimum for its environment, assuming negligible adaptation "lag" (Aitken, 2000), the degrees to which growth rhythm changes under reasonably low selection intensity within a local population may provide useful hints to the answer. Most individuals within a natural population are able to survive and complete normal life cycle functions because they are adapted to local climates. If most individuals of a selected sub-population can also survive and have normal growth, then any changes in growth rhythm are likely at a level that allows for synchronization with the local climate. Tolerable changes in growth rhythm, thus, can be used as one of the factors to determine safe seed transfer distances because the same amount of change in growth rhythm can be brought about by moving an unselected population from milder environments (Rehfeldt, 1992a).

Eastern white pine (*Pinus strobus* L.) has a natural distribution that ranges from the boreal forests of eastern Canada to Georgia, USA. Range-wide and regional provenance tests have revealed that trees of southern populations (within 2–7° in latitude) frequently outperform the local ones in growth rate (Fowler and Heimburger, 1969; Garrett et al., 1973; Genys, 1987; Li et al., 1997; Joyce et al., 2002), but with no significant differences in major adaptive characteristics, such as frost damage and survival. Potential gains in growth through seed source selection have been investigated (Garrett et al., 1973; Genys, 1987; Joyce et al., 2002); however, growth rhythm characteristics associated with superior growth have not been well studied and the effects of seed transfer on growth rhythm is not well explained.

In this study, we investigated the relationships between accumulated shoot increment and growth rhythm variables for 2-year-old greenhouse-grown seedlings and 7-year-old field trees belonging to 112 natural populations of eastern white pine in Ontario through an analysis of shoot elongation curves. The effects of selection for faster growth on the change of growth rhythm variables and their implication to geographic seed transfer in Ontario were examined.

2. Materials and methods

2.1. Population samples and test establishment

About 112 natural populations of eastern white pine were sampled from across central and southern Ontario (Fig. 1). In each of the populations, seeds were collected from more than 10 randomly selected trees that were at least 20 m apart or from at least four squirrel caches. The collection area ranged from 42.9 to 48.3° N latitude, from 74.4 to 84.7° W longitude, and from 53 to 520 m in elevation. Detailed information about the seed sources is given elsewhere (Joyce et al., 2002).

Seedlings were grown in 3.8 cm × 21 cm Ray Leach tubes filled with 1:1 commercial peat moss/vermiculite (v/v) mixture using a randomized complete block experimental design and 10-seedling row plots in the greenhouse in 1995. Growth of first year seedlings was accelerated with supplemented 16 h day

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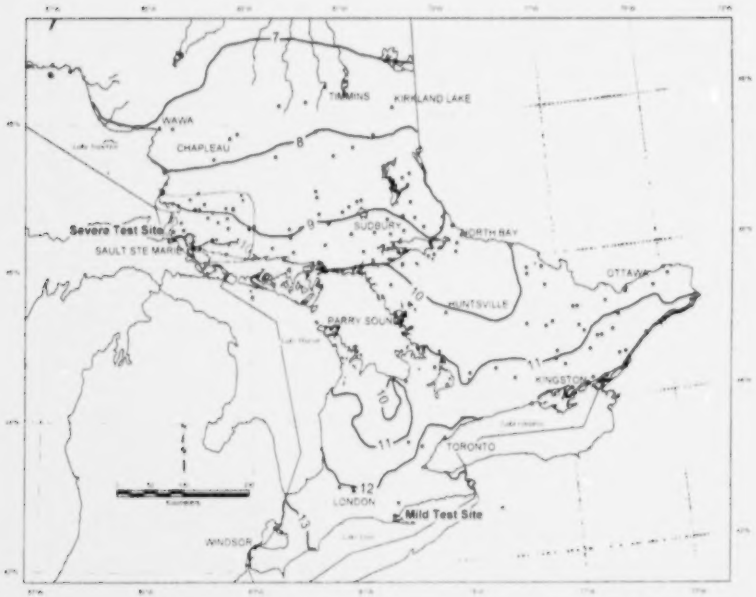

Fig. 1. Distribution of provenance samples (●), towns/cities (▲), field provenance test sites (★) and the annual mean maximum temperatures (°C) (numbered lines) in Ontario. Shaded area indicates 22 populations were merged to form a base population for selection as part of a tree improvement program.

and a temperature regime of 28 °C (day)/18 °C (night). Seedlings were fertilized with 20-8-20 at 100 ppm nitrogen once a week.

After cold storage at −5 °C through the winter, three replications of seedlings were moved back to the greenhouse to start the second growing season at 18 °C (day)/13 °C (night) temperatures and 16 h photoperiod. Seedlings were fertilized weekly with 20-20-20. Seedling height increments were measured from April 24 (onset of height growth) to June 6, 1996 (end of height growth) at 3-day intervals.

Two field tests were established at Sault Ste. Marie and Turkey Point, Ontario in the spring of 1996 (Fig. 1) using a randomized complete block design with 10-tree row plots and 4 blocks. The same 112 provenance as those studied in the greenhouse, but with a separate set of seedlings, were planted at a narrow spacing of 1.0 m × 0.5 m between rows to minimize block sizes and maintain environmental homogeneity. At the Sault Ste. Marie site, climate conditions were recorded by an on-site weather station (Fig. 2). Height increment was measured periodically from May 22 to July 26 during the growing season of 2001 at approximately 7-day interval. The Turkey Point site was not included because no repeated measurements took place at that site.

2.2. Data analysis

Growth curves of shoot elongation for the second year greenhouse seedlings and the 7-year-old trees of the Sault Ste. Marie site were individually fitted using SAS NLIN procedure (SAS Institute Inc., 1996) with a logistic function:

$$Y = a(1 + be^{-cX})^{-1} \quad (1)$$

where Y is the total height increment at day X; a, b, and c are model parameters; and e is the base of the natural logarithm.

In addition to the three model parameters, Eq. (1) was used, following Rehfeldt (1992a,b), to predict the following growth rhythm variables that describe key characteristics of shoot elongation of individual seedlings or trees:

- shoot elongation start (SES) date as indicated by the first 3 mm (age 2 days) or 3 cm (age 7 days) shoot growth;

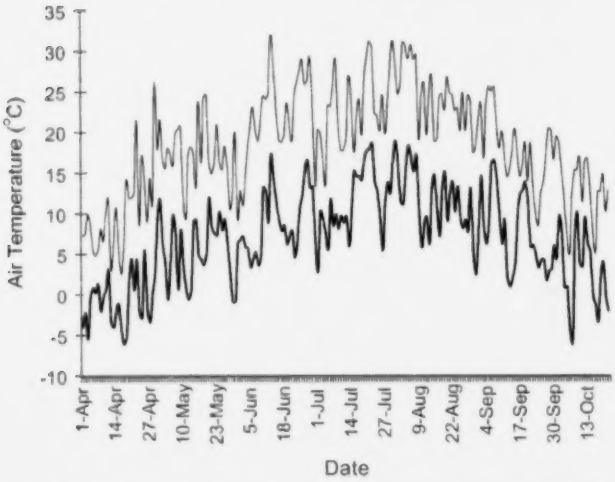

Fig. 2. Daily maximum and minimum air temperatures 1.5 m above ground at the field provenance test site in Sault Ste. Marie, Ont., in 2001.

- shoot elongation cessation (SEC) date as indicated by the last 2 mm (age 2 days) or 2 cm (age 7 days) of shoot growth;
- shoot elongation period (SEP), i.e. days between the start and end of shoot elongation;
- date that 20% of total height increment has been attained (D20%);
- date that 80% of total height increment has been attained (D80%);
- period within which the middle 60% of height increment occurs (GP60%);
- Rate of fast shoot elongation (RE), i.e. the ratio of 60% of total shoot growth to the GP60%.

Population variation in growth rhythm variables were analyzed using the linear model:

$$y_{ijk} = \mu + B_i + P_j + I_{ij} + e_{ijk} \quad (2)$$

where y_{ijk} is the phenotypic observation of the kth individual of the ith block and the jth population; μ the overall mean; B_i the effect of the ith block; P_j the effect of the jth population; I_{ij} the interaction between the ith block and the jth population; and e_{ijk} the residual of the kth individual of the ith block and the jth population. The effects of populations were treated as fixed for significance testing and, then, as random for variance component estimation. Block effects were treated as random throughout.

Spatial pattern of variation in growth rhythm among populations was modeled using multiple regression analysis with backward selection for geographic coordinate(s) or/and climate variables.

The effects of selection on growth rhythm variables within a natural population were examined by assuming 25, 50, 75, 90 and 99% culling of slow-growing individuals. Allowable changes in growth rhythm variables were calculated, assuming that after culling the population remains adapted to the local environment. These changes were compared with those of the least significant distances (LSD) among population means that statistically distinguish populations from each other. Safe geographic distance for transferring seeds from an unselected population of milder environments was, then, calculated based on the detected spatial patterns that would result in equivalent changes in population statistics of growth rhythm traits as that resulting from within population selection.

3. Results

3.1. Shoot elongation curves and growth rhythm variables

The modeled shoot elongation curves fitted data from most of the 2-year-old seedlings and the 7-year-old trees nearly perfectly. R^2 values averaged 0.994 and 0.997, respectively, for the shoot elongation curves of 3905 seven-year-old trees and 3013 two-year-old seedlings

for which complete observations were available, ranging from 0.980 to 1.0, with 86–95% of R^2 greater than 0.990. Shoot growth curves did not fit well for data from about 2.5% (77) of the seedlings and 2.8% (102) of the 7-year-old trees because of either failure to converge or irregular estimates of model parameters. These individuals were excluded from further statistical analysis.

Statistics of the estimates of shoot elongation curve parameters and the predicted shoot growth rhythm variables are given in Table 1. The effects of curve parameters on shoot elongation patterns are shown in Fig. 3, based on the mean curve parameter estimates and their standard deviations for the 7-year-old trees. Evidently, parameter *a* of the logistic function defines the maximum possible shoot elongation in the growing season (I), while parameters *b* and *c* jointly determine the shape of the growth curve (II and III) and time needed to reach the maximum. A combination of curve parameters with smaller *b* value and larger *a* and *c* values is more desirable to formulate a growth pattern that shortens the growth period and increases the shoot elongation rate (IV).

Based on the definition of the growth rhythm variables, on average, shoot elongation started around May 3 under the accelerated greenhouse growth environments used for the 2-year-old seedlings and lasted for about 28 days before shoot elongation stopped on June 1, 1996. During the rapid shoot elongation period, which accounted for the middle 60% of total shoot elongation, daily average increment was about 8.4 mm. For the 7-year-old trees grown in a field environment in Sault Ste. Marie, on average, shoot elongation started around May 14, 2001, lasted for 53 days, and ended by July 7. Daily shoot increment

Table 1
Statistics of shoot elongation curve parameters and growth rhythm variables, and the proportional contribution of population (σ^2_P), population × block interaction and residuals (σ^2_w) to phenotypic variance (σ^2_{ph})

Trait	Mean	Standard deviation	CV (%)	σ^2_P (%)	$\sigma^2_{B\times P}$ (%)	σ^2_w (%)	σ^2_{ph}
2-year-old seedlings							
a	96.58	21.95	22.73	10.10	7.56	82.34	473.50
b	93.92	39.27	41.81	5.00	4.6	90.38	1522.94
c	0.262	0.027	10.11	7.07	6.49	86.44	0.00069
SES (days)	3.9	1.5	38.461	4.31	3.22	92.47	2.1895
SEC (days)	31.9	3.1	9.719	12.93	6.37	80.69	9.4695
SEP (days)	27.9	3.7	13.26	10.99	5.35	83.66	13.3219
D20% (days)	11.8	1.3	11.02	10.78	6.40	82.82	1.7081
D80% (days)	18.7	1.6	8.56	11.76	6.44	81.81	2.6620
GP60% (days)	6.9	0.7	10.14	6.26	6.75	86.99	0.5286
RE (mm per day)	8.4	2.0	23.81	5.88	9.26	84.86	3.7446
7-year-old trees							
a	494.91	136.81	27.64	9.90	4.16	85.94	18713.3
b	58.91	29.05	49.31	4.97	4.87	90.16	834.218
c	0.092	0.011	12.12	4.87	4.10	91.03	0.00012
SES (days)	13.4	5.2	38.81	7.01	5.25	87.74	25.6937
SEC (days)	66.7	8.5	12.74	8.72	3.06	88.22	68.4165
SEP (days)	53.3	12.0	22.51	7.63	4.16	88.21	142.774
D20% (days)	27.9	3.4	12.19	10.29	2.33	87.38	10.4282
D80% (days)	47.6	3.9	8.19	9.44	2.27	88.29	13.3153
GP60% (days)	19.7	2.4	12.18	5.07	4.03	90.90	5.4437
RE (mm per day)	15.0	3.8	25.33	8.53	3.31	88.17	14.0811
Ht7	2045.1	367.3	18.80	17.96	6.21	75.83	134078.0

Note: *a*, *b* and *c* are shoot elongation curve parameters. SES, SEC, SEP, D20%, D80% GP60% and RE are the days of shoot elongation start (SES), shoot elongation cessation (SEC), shoot elongation period (SEP), 20 and 80% total increment attained (D20% and D80%), growth period of the middle 60% total shoot growth (GP60%); growth rate during the middle 60% total shoot growth (RE), and the 7-year-old total tree height (Ht7), respectively. For the 2-year-old greenhouse seedlings, days of the SES, SEC, D20% and D80% are counted from April 29, 1996, while for the 7-year-old trees, days for the SES, SEC, D20% and D80% are counted from May 1, 2001.

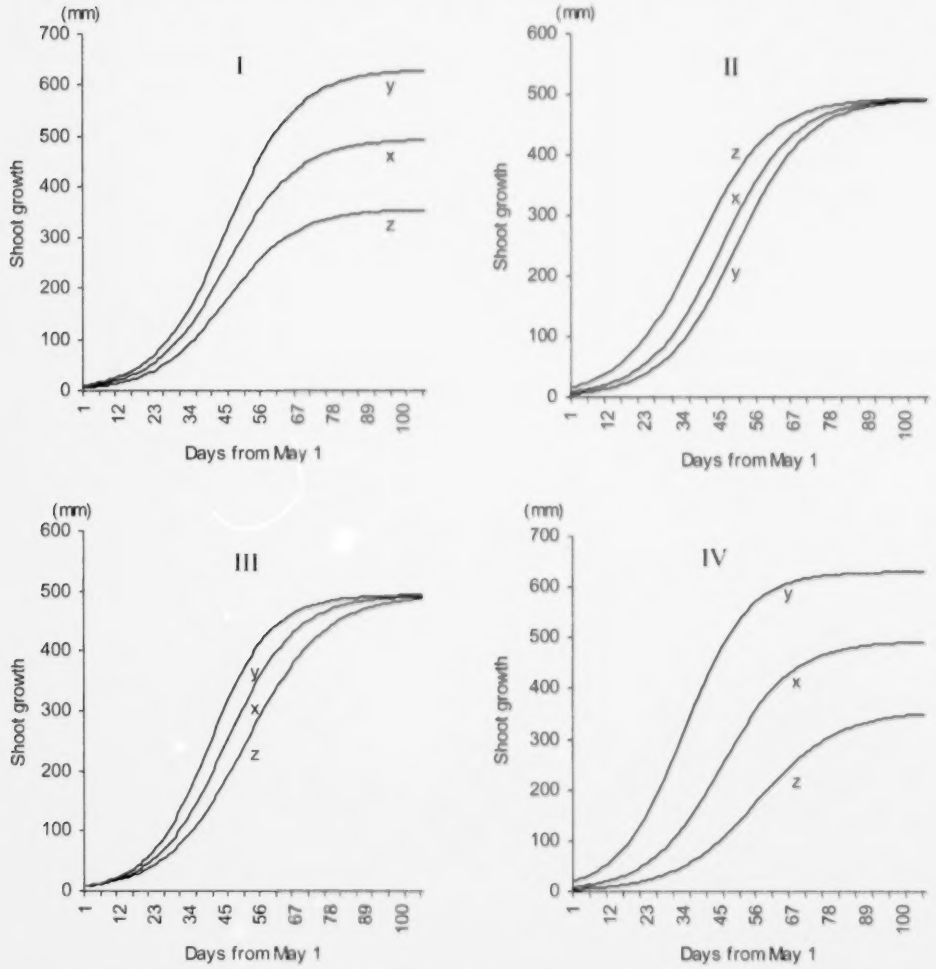

Fig. 3. Illustration of shoot elongation curves as affected by the logistic function parameters *a*, *b* and *c*. (I) *b* and *c* take the mean values of all trees while *a* takes the values of the mean (*x*), 1 standard deviation (S.D.) above (*y*) and below (*z*) the mean; (II) *a* and *c* take the means, while *b* takes the values of the mean (*x*), 1 S.D. above (*y*) and below (*z*) the mean; (III) *a* and *b* take the means, while *c* takes the values of the mean (*x*) and 1 S.D. above (*y*) and below (*z*) the mean; (IV) *a*, *b* and *c* take the means (*x*), *b* is 1 S.D. below and *a* and *c* are 1 S.D. above the means (*y*), and *b* is 1 S.D. above and *a* and *c* are 1 S.D. below the means (*z*).

averaged 15.0 mm for the middle 60% of total shoot growth. Both shoot elongation period and the rate of fast shoot elongation (RE) were nearly double for the 7-year-old trees as compared with the 2-year-old seedlings.

A correlation matrix for the three shoot elongation curve parameters and the growth rhythm variables is given in Table 2. Regardless of population, faster-growing trees tended to have a longer shoot elongation period (SEP) than the slower-growing ones, through both an earlier start and later cessation of shoot elongation. Shoot elongation potential (as indicated by curve parameter *a*) is significantly and positively correlated with the date of shoot elongation cessation (SEC) and elongation period (SEP), but negatively with the date of shoot elongation start (SES). For

Table 2
Pearson correlation among shoot elongation curve parameters and growth rhythm variables for the 2-year-old greenhouse-grown seedlings and the 7-year-old trees grown in Sault Ste. Marie at the individual tree and population levels

Trait[a]	*a*	*b*	*c*	SES	SEC	SEP	D20%	D80%	GP60%	RE	Ht7
Individual level[b]											
a		0.12	−0.13	−0.43	0.53	0.62	0.33	0.32	0.11	0.91	–
b	−0.17		0.57	0.76	−0.06	−0.36	0.62	0.25	−0.54	0.36	–
c	−0.50	0.74		0.41	−0.80	−0.84	−0.22	−0.61	−0.99	0.29	–
SES	−0.63	0.77	0.74		−0.18	−0.55	0.55	0.26	−0.40	−0.23	–
SEC	0.86	−0.20	−0.72	−0.52		0.92	0.68	0.90	0.80	0.17	–
SEP	0.87	−0.47	−0.83	−0.80	0.93		0.36	0.67	0.84	0.24	–
D20%	0.35	0.64	0.10	0.45	0.51	0.17		0.90	0.22	0.23	–
D80%	0.59	0.13	−0.50	−0.06	0.87	0.64	0.80		0.62	0.04	–
GP60%	0.47	−0.71	−0.98	−0.74	0.72	0.82	−0.11	0.50		−0.31	–
RE	0.91	0.13	−0.12	−0.38	0.64	0.61	0.44	0.43	0.08		–
Ht6	0.53	0.04	−0.15	−0.21	0.44	0.40	0.31	0.35	0.12	0.55	
Population level											
a		0.24	−0.41	−0.36	0.75	0.78	0.62	0.63	0.39	0.92	0.36
b	−0.13		0.38	0.77	0.12	−0.13	0.64	0.36	−0.37	0.42	0.07
c	−0.60	0.72		0.43	−0.84	−0.88	−0.44	−0.72	−1.00	−0.03	−0.33
SES	−0.60	0.83	0.83		−0.19	−0.48	0.37	0.13	−0.42	−0.21	−0.07
SEC	0.92	−0.09	−0.71	−0.50		0.95	0.82	0.95	0.83	0.46	0.40
SEP	0.92	−0.42	−0.86	−0.79	0.93		0.62	0.81	0.88	0.48	0.38
D20%	0.44	0.73	0.12	0.42	0.56	0.22		0.94	0.44	0.49	0.34
D80%	0.71	0.30	−0.41	−0.04	0.88	0.65	0.85		0.72	0.38	0.38
GP60%	0.58	−0.71	−0.99	−0.82	0.69	0.85	−0.13	0.41		0.01	0.31
RE	0.95	0.11	−0.34	0.40	0.82	0.76	0.56	0.67	0.30		0.27
Ht6	0.76	0.21	−0.27	−0.20	0.72	0.60	0.61	0.69	0.23	0.81	

[a] The definition of traits is the same as in Table 1 except that the 6-year-old tree height is used here to avoid auto-correlation.
[b] The upper diagonal of a correlation matrix is for the 2-year-old greenhouse seedlings and the lower diagonal of a correlation matrix is for the 7-year-old field trees grown in Sault Ste. Marie. All correlation coefficients are significant ($\alpha \leq 0.01$) at the individual level. At population level, correlation coefficients (r) are significant at the probability levels of $\alpha \leq 0.01$ when $|r| > 0.24$ and $\alpha \leq 0.05$ when $|r| > 0.19$.

both the 2-year-old seedlings and 7-year-old trees, the estimate of growth curve parameter c was highly negatively correlated to the period of the middle 60% shoot growth (GP60%), SEC and SEP at both the individual and population levels (Table 2). Faster-growing trees and populations also had higher RE during the rapid elongation period (i.e. GP60%). But, RE was only moderately positively correlated to curve parameter b and negatively with c, indicating that selection on RE will not necessarily bring about dramatic changes in b and c. Moderately strong correlation between estimates of parameters a and c (−0.40 to −0.60) and between b and c (0.38–0.72) at the individual and population levels indicated that fast-growing trees and populations would generally have a longer growth period. This is confirmed by the significant correlation between the 6-year-old field tree height and the growth rhythm variables of the 2-year-old seedlings and the seventh year shoot elongation. There were, however, exceptional trees that had desirable shoot growth curves, i.e. with smaller estimate of b and larger estimates of a and c, which formulated shoot growth curves of larger shoot growth potential and shorter growth period.

3.2. Population variation

Geographic populations showed significant differences in the estimates of shoot elongation curve parameters as well as the growth rhythm variables for both the 2-year-old seedlings and the 7-year-old trees. When treated as fixed effects, both population and population × block interaction were significant at the probability level of $\alpha = 0.01$. When treated as random, however, population accounted for less than 5.0% of the total variation in curve parameter

estimates of *b* and *c* and less than 10.5% for other growth rhythm variables of the 7-year-old trees (Table 1). Population variation was higher for shoot elongation cessation than start, which accounted for 8.7–12.9% of the total phenotypic variance. Shoot elongation period was somewhere in between. In general, about 83–92% of the phenotypic variation of growth rhythm variables resided within population. The large sample size used in this study apparently enhanced the statistical power to detect small differences among population means when treated as fixed effects. In comparison, population variation in growth potential as represented by curve parameter *a* and 7-year total height, was relatively larger, accounting for 10–18% of the total variation. A significant population × block interaction was detected, probably a result of the tree measurement process. There was a 1-day delay per block in shoot increment measurement from block 1 through block 4.

Despite the fact that population had accounted only for a relatively small proportion of the total phenotypic variation, spatial pattern of variation in growth rhythm was evident. Table 3 shows the Pearson correlations among population means of growth rhythm variables and the geographic and climatic variables of population origins. These significant correlation coefficients suggested a clinal pattern of population variation in growth rhythm traits. In general, southern populations from milder environments tended to have smaller estimates of *c* and larger estimates of *a* and *b* of the shoot elongation curve parameters, which led to delayed shoot elongation cessation and thus a longer elongation period. Spatial pattern for shoot elongation start (SES) was, however, less evident since SES was not significantly correlated with latitude or several other thermal variables (Table 3). Based on the multiple regression analysis using the backward selection approach (SAS Inc., 1996), geographic and climatic variables could explain up to 50% of the variation among populations in shoot elongation cessation (SEC) and shoot elongation period (SEP).

Although the shoot elongation curves for the 2-year-old seedlings and that of the 7-year-old trees were fitted based on separate sets of individuals of same populations, there was, however, significant correlation among growth rhythm variables between the two sets of trees when population means were used (Table 4). For example, smaller values of population means in the *c* parameter of the shoot elongation curve of the 2-year-old seedlings were good predictors of later shoot growth cessation, longer elongation period, and faster shoot growth rate for populations of the 7-year-old trees in the field. Also, population means in SEC, SEP D20%, D80%, and GP60% of the 2-year-old seedlings were significantly correlated with total height of the 6-year-old field trees.

Table 3
Pearson correlation between population means of growth rhythm variables and geographic coordinates and climatic variables of the population origins for the 7-year-old trees grown in Sault Ste. Marie[a]

Trait[b]	LON	LAT	GSL	MT	MINT	MAXT	JDS	JDE	ADD3	ADD4
a	0.60	−0.57	0.55	0.55	0.52	0.57	−0.58	0.53	0.59	0.58
b	0.08	−0.20	0.21	0.21	0.21	0.22	−0.21	0.20	0.21	0.21
c	−0.28	0.22	−0.25	−0.24	−0.23	−0.24	0.25	−0.24	−0.25	−0.25
SES	−0.21	0.09	−0.05	−0.05	−0.04	−0.06	0.08	−0.04	−0.09	−0.08
SEC	0.58	−0.59	0.61	0.60	0.58	0.61	0.62	0.59	0.63	0.62
SEP	0.50	−0.46	0.46	0.45	0.43	0.47	0.48	0.44	0.48	0.48
D20%	0.43	−0.55	0.59	0.59	0.57	0.59	0.59	0.58	0.59	0.59
D80%	0.53	−0.61	0.67	0.66	0.64	0.66	0.67	0.65	0.66	0.66
GP60%	0.26	−0.20	0.23	0.22	0.21	0.22	0.24	0.22	0.23	0.23
RE	0.60	−0.59	0.55	0.55	0.53	0.57	0.58	0.53	0.59	0.59

Climatic variables are: latitude (LAT); longitude (LON); growing season length (GSL); annual mean minimum (MINT) and maximum (MAXT) temperatures; Julian day of growing season start (JDS) and end (JDE); aggregated degree days in the growing period 3 (ADD3) and 4 (ADD4); and mean temperature in GP3 (MTP3). Here, GP1 = before growing season start, GP2 = the first 6 weeks of growing season, GP3 = the whole growing season, and GP4 = GP3 − GP2.

[a] Correlation coefficients (r) are significant at the probability levels of $\alpha \leq 0.01$ when $|r| > 0.24$ and $\alpha \leq 0.05$ when $|r| > 0.19$.

[b] The definition of traits is the same as in Table 1.

Table 4
Correlation between growth rhythm variables of the 2-year-old seedlings and that of the 7-year-old trees at the population level

Trait[a]	*a*	*c*	SEC	SEP	D20%	D80%	GP60%	RE
a	0.28**	−0.26**	0.31**	0.30**	0.26**	0.30**	0.25**	0.20*
b	ns	−0.19*	ns	ns	ns	0.20*	0.19*	ns
SEC	0.26**	−0.32**	0.36**	0.33**	0.32**	0.36**	0.30**	ns
SEP	0.24**	−0.21*	0.26**	0.25**	0.22*	0.24**	0.19*	ns
D20%	ns	−0.37**	0.37**	0.32**	0.34**	0.40**	0.36**	ns
D80%	ns	−0.38**	0.41**	0.36**	0.37**	0.42**	0.37**	ns
RE	0.28**	−0.28**	0.32**	0.30**	0.27**	0.31**	0.27**	0.20*
Ht7	0.37**	−0.33**	0.40**	0.38**	0.34**	0.38**	0.31**	0.28**

Note: those in the columns are the seedling variables and the rows are the 7-year-old tree variables.
[a] The definition of traits is the same as in Table 1.
* Significant levels are $\alpha \leq 0.05$.
** Significant levels are $\alpha \leq 0.01$.

3.3. Selection effects on growth rhythms

To examine the effects of individual selection on changes in population statistics in growth rhythm variables, 22 populations within 0.5° in latitude and 0.8° in longitude from Sault Ste. Marie (Fig. 1) were merged to form a larger base population for selection. The geographic area of these 22 populations would normally fall into one breeding zone of an operational tree improvement program. The effects of culling 25, 50, 75, 90, and 99% of the slow-growing individuals on population statistics in growth rhythm variables are summarized in Table 5. Clearly, population statistics in shoot elongation curve parameters as well as the growth rhythm variables were substantially changed by even a moderately low culling intensity. For example, when 25% of the trees are culled, the average date of shoot elongation cessation was delayed for about 3.3 days and shoot elongation period extended for about 5 days. These numbers increased to 5.7 and 8.1 days, respectively, when 50% of the population was culled. Interestingly, at the 25% cull level, changes in population statistics of most shoot growth rhythm variables had exceeded the values calculated from the least significant distance at the probability level of $\alpha = 0.2$, i.e. LSD(0.2) (Rehfeldt, 1979). At a 50% cull level based on growth, these changes had exceeded that of LSD(0.1) (Table 5).

Table 5
Average changes of population statistics in shoot elongation curve parameters and growth rhythm variables caused by within population culling of slow-growing individuals

Culling (%)	Growth curve parameter			SES (days)	SEC (days)	SEP (days)	RE (mm)
	a	*b*	*c*				
0	494.91	58.91	0.0924	13.4	66.7	53.3	15.1
25	+60.87	−2.70	−0.0027	−1.6	+3.3	+4.9	+1.5
50	+110.59	−3.55	−0.0043	−2.4	+5.7	+8.1	+2.7
75	+166.89	−3.78	−0.0059	−3.3	+8.2	+11.5	+4.0
90	+219.38	−6.14	−0.0077	−4.4	+10.3	+14.7	+5.1
99	+312.28	−11.04	−0.0100	−6.7	+13.1	+19.7	+7.2
LSD(0.2)	48.88	10.81	0.0040	1.9	2.9	4.3	1.3
LSD(0.1)	62.78	13.88	0.0052	2.4	3.7	5.5	1.7
LSD(0.05)	74.87	16.56	0.0062	2.9	4.4	6.6	2.0

Note: the definition of traits is the same as in Table 1. Twenty-two populations within the vicinity of Sault Ste. Marie (see Fig. 1) were merged to form a base population for selection. LSD(α) is the least significant distance among population means at the probability level of $1 - \alpha$ in a multiple comparison analysis.

Table 6
Spatial models to explain population variation in shoot elongation cessation and period as well as safe seed transfer distances under different adaptation assumptions

Trait[a]	Full model		Simple regression model						Culling (%)	Allowable change	Equivalent seed transfer distance		
	R^2	Variable[b]	Add3		GSL		LAT				Add3 (degree days)	GSL (days)	LAT ( )
			R^2	b	R^2	b	R^2	b					
SEC	0.491	LAT, JDS, JDE, TP2, TP3, ADD4, MTP3	0.39	0.008	0.37	0.123	0.35	1.49	25	+3.3	412	26.8	2.21
									50	+5.7	712	46.3	3.8
SEP	0.364	LONG, JDS, TP4, ADD4, MINT, MAXT	0.23	0.009	0.21	0.130	0.20	1.62	25	+4.9	544	37.7	3.0
									50	+8.1	967	62.3	5.0

[a] The definition of traits is the same as in Table 1.

[b] Climatic variables are: latitude (LAT); longitude (LON); growing season length (GSL); annual mean minimum (MINT) and maximum (MAXT) temperatures; Julian day of growing season start (JDS) and end (JDE); aggregated degree days in the growing period 3 (ADD3) and 4 (ADD4); total precipitation in growing period (GP) 2 (TP2), 3 (TP3) and 4 (TP3); and mean temperature in GP3 (MTP3). Here, GP1 = before growing season start, GP2 = the first 6 weeks of growing season, GP3 = the whole growing season, and GP4 = GP3 − GP2.

3.4. Spatial seed transfer distances

Spatial patterns of variation suggest that populations originating from southern Ontario with better thermal conditions would have characteristics typical of fast-growing trees of northern populations, such as smaller estimates of curve parameter *c*, delayed shoot elongation cessation date, and extended elongation period (Table 3). Based on an assumption that changes in growth rhythm variables brought about by 25 or 50% culling of the natural population in the Sault Ste. Marie area are still within a level that maintains acceptable adaptation to the local climate, corresponding seed transfer distances were estimated as per description in Section 2 (Table 6). Within population selection with an intensity as low as 25% culling of the slowest growers, resulted in changes in shoot elongation cessation and period equivalent to moving an unselected population more than 2 in latitude south of Sault Ste. Marie.

4. Discussion

Eastern white pine growing in Sault Ste. Marie, Ontario, has a relatively short period for shoot elongation. Under the local weather conditions in 2001 (Fig. 2), the average shoot elongation period lasted for less than 2 months, starting in mid-May and ending in early July. This early shoot elongation cessation provided the new shoot growth sufficient time to complete the process of hardening and cold acclimation given that the first fall frost did not come until early October (Fig. 2). The synchronization between growth rhythm and climate variables, and probably also the cold tolerance capacity of eastern white pine (Lu et al., in press), during the past 7 years resulted in no visible frost damage to all populations and trees in the field provenance trial.

Estimates of shoot elongation curve parameters and predicted growth rhythm variables varied both among and within populations of eastern white pine. Results were consistent between the 2-year-old greenhouse seedlings under controlled, growth-accelerating conditions and the 7-year-old trees growing in the field, although the two studies involved a separate set of individuals from the same populations. Faster-growing trees and populations generally tended to have higher shoot growth rates as well as extended growth periods through both an earlier start and later cessation of shoot elongation. Population means in curve parameter *a* and *c* estimates, shoot elongation cessation, and shoot elongation period of the 2-year-old greenhouse seedlings were good predictors of the growth rhythm variables of the 7-year-old trees (Table 4), which implies the stability in growth rhythm traits at the population level.

Although among population differences were statistically significant, about 83–92% the phenotypic variation in growth rhythm variables resided within populations. Population accounted for less than 5.5% of the total variation in curve parameter estimates of *b* and *c* and less than 13% for other growth rhythm variables for the 2-year-old seedlings and 7-year-old trees. This is smaller than that reported among population variation in growth potential of eastern white pine (Fowler and Heimburger, 1969; Garrett et al., 1973; Genys, 1987; Li et al., 1997; Joyce et al., 2002) and in growth rhythms of the western white pine (*Pinus monticola*) (Rehfeldt et al., 1984). Similar results were reported in a previous regional provenance test of eastern white pine in Quebec (Li et al., 1997), in which among population variation in third year bud burst date accounted for 7.78% of the total variation with 83.23% residing within populations. High level of within population variation in growth rhythm was also reported in the genus of *Picea* (Pollard and Ying, 1979; Skrøppa, 1982). Although explanation for the high levels of within and low levels of between population variation in growth rhythm variables is unclear given the selection forces that influence growth rhythm (Partanen and Beuker, 1999), the results, nevertheless, favor minimal impacts of geographic seed transfer on the alteration of growth rhythms.

Spatial patterns of population variation in growth rhythm variables of eastern white pine seemed to follow a north–south clinal trend in eastern Ontario, parallel to that of growth potential (Joyce et al., 2002) and cold hardiness (Lu et al., in press). Population means of shoot elongation cessation (SEC) date and shoot elongation period (SEP) were highly negatively correlated with latitude and several thermal variables (Table 3). These trends seemed to be consistent with those findings in several other forest tree species in shoot elongation cessation

(Ekberg et al., 1994; Westin, 1999; Partanen and Beuker, 1999).

As a result of strong correlation between growth rate and growth variables at both the individual and population level, selection for increased growth will delay the time of shoot elongation cessation and expand the shoot elongation period. An 8-day expansion in shoot elongation period is expected when half of the slow-growing individuals are culled. The mean shoot elongation period can, however, be increased by nearly 20 days if high selection intensity of 99% culling is applied. In operational tree improvement programs, high mass selection intensity with less than 1% of individuals being selected is not unusual (Park and Simpson, 1995; White et al., 1999). This implies that the mean shoot elongation date would not be reached until July 20. Whether or not such delay can significantly increase the vulnerability of eastern white pine to fall frost damage may depend on the time needed for trees to get sufficient degree of cold hardiness and the weather conditions of the planting sites. In the field provenance test of Sault Ste. Marie, no visible cold damage was observed during a 7-year period. Thus, at 75 or 50% mass selection intensity, no detectable risk of maladaptation would be expected from poor synchronization between shoot growth rhythm and climate variables. It, therefore, seems quite reasonable that the changes in shoot growth rhythm variables at 25 or 50% culling on growth potential could be used to estimate a safe seed transfer distance from a milder environment that will bring about the same amount of change. Based on spatial regression analyses, it was apparent that seed sources of eastern white pine from populations 2° latitude or more south of a regeneration site or 26 days in growing season length could be safe with respect to synchronization in shoot growth rhythm.

Rehfeldt (1979) proposed the use of LSD(0.2) as the acceptable change to calculate safe seed transfer distances. Our results have shown that this approach may be too conservative and may not necessarily yield reasonable estimates. Because LSD(0.2) is heavily affected by the sample sizes of individuals within a population and by experimental precision, theoretically, LSD(0.2) can become indefinitely smaller when the number of trees per population gets larger. Under such circumstances, LSD(0.2) tends to underestimate safe seed transfer distances.

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